Tropical Zoology 22: 195-204, 2009

Chemical communication in competitive interactions among tropical stream detritivores

K. ALLAN [1], L. BOYERO [1,2,3,4] and R.G. PEARSON [1]

[1] *School of Marine and Tropical Biology, James Cook University, Australia*
[2] *Wetland Ecology Group, Estación Biológica de Doñana-CSIC, Avda Americo Vespucio s/, Isla de la Cartuja, E-41092, Spain*
[3] *Smithsonian Tropical Research Institute, Panama*

The role of chemical communication among competitors in streams is virtually unknown, especially in tropical streams. In this study, we experimentally examined the ability of four tropical invertebrate shredders (*Anisocentropus kirramus* Neboiss 1980, *Lectrides varians* Mosely 1953, *Triplectides gonetalus* Moser & Neboiss 1982 and *Atalophlebia* sp.) to detect and respond to chemical cues from competitors of the same species (conspecifics) or other species (heterospecifics — the other three species plus the crayfish *Cherax cairnsensis* Riek 1969). Behavioural trials indicated a short-term response (a reduction in activity) to the addition of conspecific chemical cues but not to those of heterospecifics, including the crayfish. Litter breakdown experiments showed no mid-term effects of chemical cues from conspecifics or heterospecifics on breakdown rates. Our results indicate that chemical communication among tropical stream shredders is weak, suggesting that hydrodynamic cues and physical contact may be primary mechanisms mediating competitive interactions among these organisms.

KEY WORDS: chemical cues, biotic interactions, competition, leaf litter breakdown, shredders, tropical streams.

INTRODUCTION

Stream communities have been traditionally seen as shaped by environmental forces, while biotic interactions have been considered secondary and have thus received little attention (MCAULIFFE 1984). Processes that facilitate biotic interactions (e.g. behavioural strategies and responses) remain largely unknown or poorly understood in streams (KOHLER 1992). As visual and auditory senses often prove less effective in aquatic environments, chemical communication usually plays an important role in the recognition of predators, alarm signals, food, conspecifics and migration (BRONMARK &

[4] Corresponding author: Luz Boyero, School of Marine and Tropical Biology, James Cook University, Townsville, 4811 QLD, Australia (E-mail: luz.boyero@jcu.edu.au).

Hansson 2000, Burks & Lodge 2002, Pollock & Chivers 2004). Responses of aquatic invertebrates to chemical cues from other organisms include changes in foraging behaviour and movement (Kuhara et al. 2000, McIntosh et al. 2004), altered life history traits (Peckarsky et al. 2001, 2002) and altered drift behaviour (McIntosh et al. 1999).

The majority of research on chemical communication in streams has investigated predator/prey interactions (e.g. Short & Holomuzki 1992, Turner et al. 2000, Peckarsky et al. 2002, Miyasaka et al. 2003, McIntosh et al. 2004), while research on the role of chemical cues in competitive inter- and intra-specific interactions is scarce. It has been suggested that most chemical cues operating in freshwaters occur between species rather than among individuals of the same species (Burks & Lodge 2002). Evidence exists of recognition of conspecific alarm cues among freshwater biota, but these cues are usually related to predation risk rather than competition (e.g. Scrimgeour et al. 1994, Huryn & Chivers 1999, McCarthy & Fisher 2000). Furthermore, the majority of research on competitive interactions has focused on grazers or collectors (e.g. McAuliffe 1984, Hemphill 1988, Kohler 1992, Harding 1997, Kuhara et al. 2000, Cross & Benke 2002), while studies on detritus-based food webs are scarce. Interactions between and within species operating in detritus-based systems may well be different from those operating in other systems due to differences in the type and use of resources, as occurs for predator-prey interactions (Boyero et al. 2008).

In headwater forest streams, where riparian vegetation is dense and primary production limited, leaf litter and woody debris are the basis of the food web (Pearson & Tobin 1989). Detritivores (particularly shredders) play a key role in the energy and nutrient transfer in such streams in the temperate zones (Graça 2001). While some studies suggest that shredders are scarce in tropical streams (e.g. Dobson et al. 2002), they are common in streams of the Australian wet tropics (Cheshire et al. 2005) — they can be locally very dense (e.g., many individuals of more than one species per leaf (unpubl. data) and show strong intraspecific interactions (Boyero & Pearson 2006). These streams therefore offer an ideal opportunity to examine the role of chemical communication on species interactions and its consequences on ecosystem functioning in detritus-based tropical systems. Moreover, studies on tropical streams are particularly desirable because most of our knowledge of stream macroinvertebrate ecology comes from temperate studies (Boyero et al. 2009).

The objectives of this study were to determine: (1) if shredder species are able to detect and respond behaviourally to chemical cues from conspecifics and heterospecifics (other shredders); and (2) if detection and response to these chemical cues has an effect on their rates of leaf breakdown.

METHODS

Shredder species and study area

We collected experimental animals at Birthday Creek (18°59'S, 146°10'E) and Camp Creek (also called Little Birthday Creek; 18°58'S, 146°10'E), within the Palu-

ma Range National Park, north-eastern Queensland, Australia. The streams are third order, upland rainforest streams (~ 800 m a.s.l.) and display seasonal flow and temperature regimes, like other streams in the region (Pearson et al. 1986).

We investigated interactions among the four most common shredder species in these streams: *Anisocentropus kirramus* Neboiss 1980 (Trichoptera Calamoceratidae), *Lectrides varians* Mosely 1953, *Triplectides gonetalus* Morse & Neboiss 1982 (Trichoptera Leptoceridae), and *Atalophlebia* sp. (Ephemeroptera Leptophlebiidae). A previous study showed the existence of intraspecific competitive interactions in these species, with increased densities of individuals causing a decrease in individual leaf breakdown rates (Boyero & Pearson 2006). In addition, these shredders were found to reduce their activity in response to chemical cues from predatory fish (Boyero et al. 2008). In this study, we examined the response of these species to the presence of chemical cues from individuals of the same species or from any of the other three shredder species. Additionally, we examined the effect of the presence of chemical cues from the crayfish *Cherax cairnsensis* Riek 1969 (Parastacidae), which is another important shredder and also a potential predator of insect shredders in these streams (Cheshire et al. 2005, Boyero et al. 2006).

We collected approximately 150 individuals (late instars) of each species from litter patches in pools and riffles during the late wet season (March-April, 2005) when stream flow was low and water temperature ranged between 18 and 20 °C. Individuals were placed in containers with stream water and leaf litter and, once in the laboratory, they were acclimated for a few days in containers filled with commercial spring water and fed with *Apodytes brachystylis* Mueller 1875 (Icacinaceae) leaves collected from the riparian zone of Birthday and Camp Creeks.

Behavioural experiment

We placed each experimental individual in a plastic container (25 × 11 cm) filled with 200 ml of commercial spring water and allowed it to acclimate for 5 min. Then we observed the individual for 3 min and measured the time (in seconds) that the animal was active — crawling, swimming (only mayflies) or moving its legs. We then added 5 ml of water with chemical cues (see below) and immediately quantified the activity of the individual for another 3 min. We subjected 10 individuals of each species to each of 6 treatments (chemical cues from *A. kirramus*, *L. varians*, *T. gonetalus*, *Atalophlebia* sp, crayfish; and controls — water only, with no chemical cues), so 60 individuals of each species were tested in total.

To obtain the chemical cues, we kept 20-30 individuals of each insect shredder species (or 1 crayfish) in a container with commercial spring water and leaves of *A. brachystylis*. Control containers had leaves but no animals. If animals pupated or died they were removed immediately from the containers. Temperature was maintained at 20 °C and a 12:12 hr light-dark photoperiod was simulated to reflect natural conditions.

The addition of water with chemical cues may introduce some disturbance due to visual or hydrodynamic cues, causing a reduction in activity. However, no animals were detached from the substrate during this process, and the controls underwent the same level of disturbance.

Leaf breakdown experiment

We placed each experimental individual in a plastic container filled with 150 ml of commercial spring water and one leaf of *A. brachystylis*, previously air-dried and

weighed. Once a day, we added 5 ml of water with chemical cues from *A. kirramus*, *L. varians*, *T. gonetalus*, *Atalophlebia* sp., crayfish, or without chemical cues (controls), obtained as described above. After 7 days, leaves and animals were oven-dried for 48 hr and weighed to the nearest mg. The total number of replicates per species per treatment was 4-10, depending on availability of animals (with a total of 283 animals tested: 72 *A. kirramus*, 78 *L. varians*, 69 *T. gonetalus* and 64 *Atalophlebia* sp.).

Statistical analysis

For the behavioural experiment, we analyzed the activity of individuals, measured as the time (in seconds) the animal was active. We compared activity before and after the addition of chemical cues, among species, and between treatments and controls. We considered 3 treatments: conspecifics (chemical cues from individuals of the same species); heterospecifics (chemical cues from individuals of the other 3 insect species); and crayfish (chemical cues from individuals of *C. cairnsensis*). We performed three 3-way ANOVAs, followed by post-hoc Tukey tests, each comparing one of the three treatments with controls.

For the leaf breakdown experiment, we analyzed the leaf mass loss (LML) (initial minus final leaf mass, in mg) per mg of shredder. We examined variation of LML per mg of shredder (log-transformed) among species and between treatment and controls, as above, by 2-way ANOVAs, followed by post-hoc Tukey tests.

RESULTS

Activity was always higher before than after the addition of water with chemical cues (without cues in the case of controls), although this reduction in activity varied among species (Table 1), being higher in *T. gonetalus* and *A. kirramus* and lower in the other two species (Fig. 1). Differences among species were also significant (Table 1), with activity highest in *L. varians*, followed by *A. kirramus* and *T. gonetalus* (which were not significantly different from each other), being *Atalophlebia* sp. the least active species (Fig. 1). The reduction in activity after the addition of chemical cues from conspecifics was higher than the reduction in activity after adding water in controls, but the reduction in activity after adding chemical cues from heterospecifics or crayfish did not differ from controls (Table 1, Fig. 1).

Leaf mass loss (LML) per mg of shredder varied among species (Table 2), being highest in *L. varians* followed by *A. kirramus*, *T. gonetalus*, and *Atalophlebia* sp. (Fig. 2). There were no differences in LML per mg of shredder between controls and treatments in any case (Table 2).

DISCUSSION

Our results show that insect shredders are able to detect chemical cues from conspecifics and respond to them by immediately reducing their activity. Moreover, Fig. 1 suggests that this difference is greater in the most active

Table 1.

Results of ANOVA on the variation in activity of shredders (time in seconds that the animal is crawling, swimming or moving its legs) before/after the addition of chemical cues (B/A); between controls and treatment (addition of chemical cues from conspecifics, heterospecifics, or crayfish); and among species (*Anisocentropus kirramus*, *Lectrides varians*, *Triplectides gonetalus* and *Atalophlebia* sp.).

	df	SS	F	*P*
Controls/Conspecifics				
B/A	1	32376.1	17.53	**<0.0001**
Treatment	1	8732.0	4.73	**0.0313**
Sp.	3	150634.8	27.19	**<0.0001**
B/A × Treatment	1	2016.4	1.09	0.2978
B/A × Sp.	3	15528.1	2.80	0.0420
Treatment × Sp.	3	6942.2	1.25	0.2928
B/A x Treatment × Sp.	3	1503.6	0.27	0.8459
Error	144	265902.6		
Controls/Heterospecifics				
B/A	1	30702.3	16.38	**<0.0001**
Treatment	1	4195.2	2.24	0.1357
Sp.	3	231150.8	41.11	**<0.0001**
B/A × Treatment	1	100.6	0.05	0.8170
B/A × Sp.	3	12609.5	2.24	0.0834
Treatment × Sp.	3	3178.0	0.57	0.6383
B/A × Treatment × Sp.	3	1988.9	0.35	0.7865
Error	144	566019.5		
Controls/Crayfish				
B/A	1	30277.5	13.64	**0.0003**
Treatment	1	1045.5	0.47	0.4937
Sp.	3	155436.8	23.33	**<0.0001**
B/A × Treatment	1	1519.1	0.68	0.4095
B/A × Sp.	3	3033.3	0.46	0.7139
Treatment × Sp.	3	2892.7	0.43	0.7288
B/A × Treatment × Sp.	3	7474.1	1.12	0.3423
Error	144	319744.5		

species *A. kirramus* and *L. varians* (Boyero et al. 2006a), which supports Jonsson & Malmqvist's (2003) finding of stronger intraspecific competition in more active shredder species in temperate streams.

This reduction in activity was, however, not reflected in the rates of shredding, which were similar in the presence or absence of chemical cues from conspecifics over a 1-week experiment. A previous study showed that leaf breakdown rates per capita in the four species studied here decreased

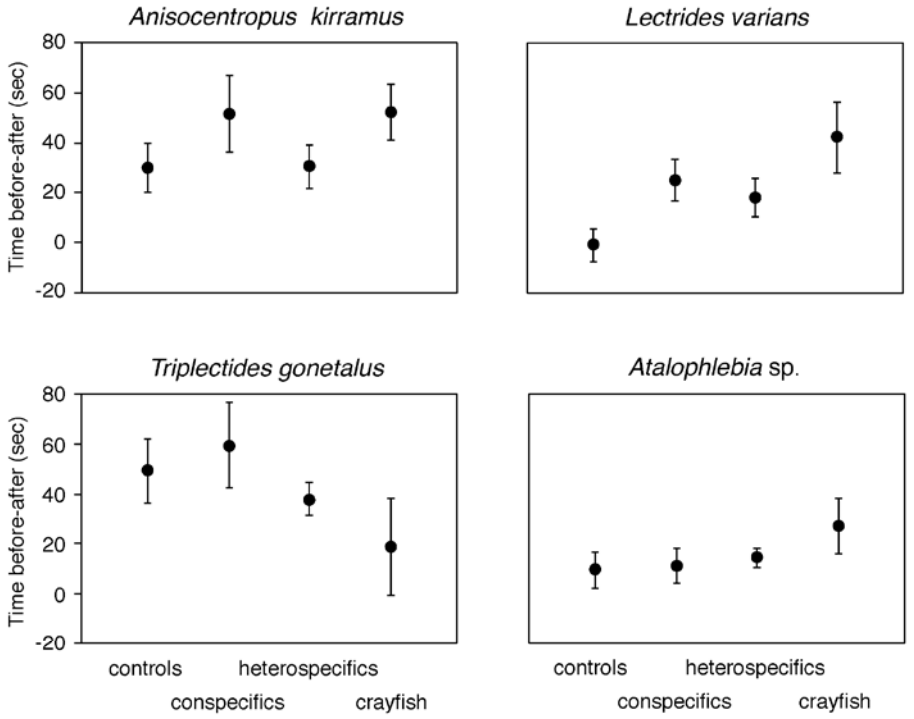

Fig. 1. — Activity of shredders: difference in time (seconds ± SE) the animal is moving in a 3-min period before and after the addition of water with chemical cues from conspecifics, heterospecifics (other insect shredder species) or crayfish; in controls, only water was added.

exponentially when other individuals of the same species were present (Boyero & Pearson 2006). The combined results of both experiments suggest that, although shredders are able to detect conspecifics chemically, their shredding efficiency is not affected unless there are visual interactions or, more likely, tactile encounters. Interference competition by physical encounters has previously been reported among species of collectors and grazers (McAuliffe 1984, Hemphill 1988), and it is likely to occur in *A. kirramus* and *L. varians*, individuals of which have been observed to interact with each other in the laboratory, even feeding on each other's cases despite being provided with leaves, and many individuals of both species have frequently been observed in the field feeding on a single leaf (Boyero & Pearson 2006).

Another explanation for the absence of a medium-term effect of conspecific chemical cues on leaf breakdown rates is that individuals get used to the presence of chemical cues linked to the physical absence of conspecifics, and any immediate effect of these cues in animal activity is diluted over the time of the experiment. Although there is evidence of a learned responsiveness of aquatic macroinvertebrates to chemical stimuli from predators (Chivers et al. 1996), a learned responsiveness to chemical cues from con-

Table 2.

Variation in leaf mass loss per mg of shredder between controls and treatment (addition of chemical cues from conspecifics, heterospecifics, or crayfish) and among species (*Anisocentropus kirramus*, *Lectrides varians*, *Triplectides gonetalus* and *Atalophlebia* sp.).

	df	SS	F	*P*
Controls/Conspecifics				
Treatment	1	0.01	0.24	0.6258
Sp.	3	6.34	52.99	**<0.0001**
Treatment × Sp.	3	0.06	0.53	0.6671
Error	62	2.47		
Controls/Heterospecifics				
Treatment	1	<0.01	0.26	0.6113
Sp.	3	9.31	51.01	**<0.0001**
Treatment × Sp.	3	0.15	0.81	0.4919
Error	62	9.18		
Controls/Crayfish				
Treatment	1	0.06	1.41	0.2395
Sp.	3	6.57	54.00	**<0.0001**
Treatment × Sp.	3	0.11	0.90	0.4440
Error	62	2.92		

specifics has not been described, other than the response to alarm cues from injured conspecifics (e.g. PIJANOWSKA & KOWALCZEWSKI 1997).

In contrast to the immediate reaction to chemical cues from conspecifics, shredders did not seem to detect or respond to cues from other shredder species, even from the crayfish *Cherax cairnsensis*, which is also considered a potential predator (CHESHIRE et al. 2005). Benthic crustaceans, including crayfish, have been reported in several studies as senders of chemical cues (BURKS & LODGE 2002). In our experiment, chemical cues of *C. cairnsensis* elicited no response from insect shredders, and thus it was not chemically recognized as a competitor or as a predator. This contrasts with previous results with the predatory fish *Melanotaenia splendida* (Peters 1866), which induced a dramatic reduction in the activity of the same shredder species (BOYERO et al. 2008). Although experimental conditions could have affected the nature or concentration of crayfish chemicals (e.g. because of a diet restricted to leaves or reduced mobility), our results suggest that *C. cairnsensis* does not predate on shredders. This could be due to the protective case of these shredders (see BOYERO et al. 2006b), especially *T. gonetalus*, whose case is a hollow stick up to 10 times greater than its body size (pers. obs.). *A. kirramus* makes its case from two leaf pieces, usually cut from a tough and non-palatable species that might be also avoided by the crayfish. The case of *L. varians*, in contrast, is made of soft leaves, and individuals are smaller than

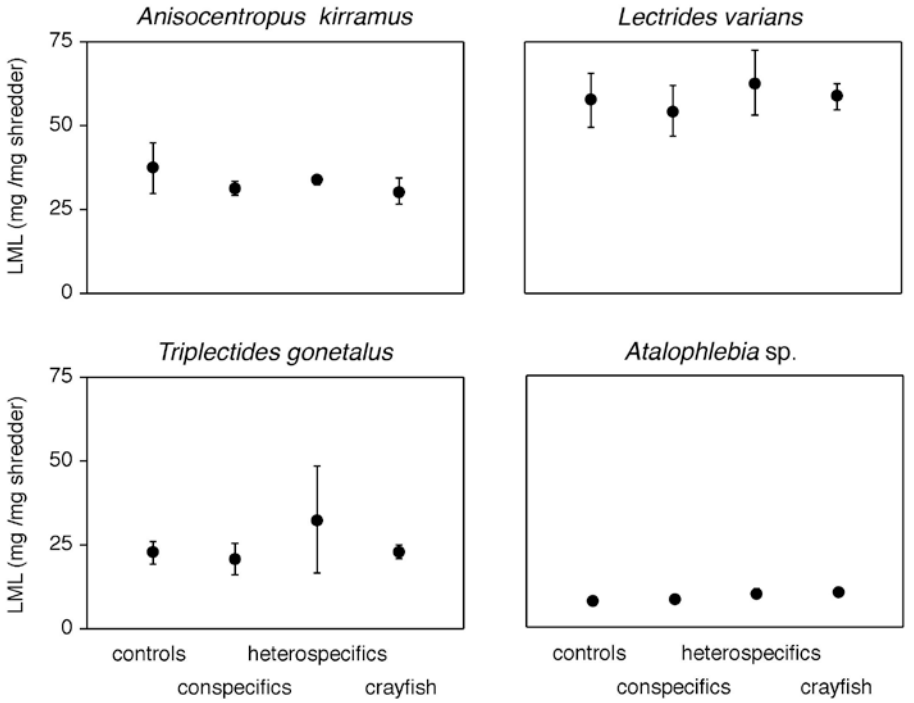

Fig. 2. — Leaf mass loss (LML) per mg of shredder in a 1-week experiment where chemical cues from conspecifics, heterospecifics (other insect shredder species) or crayfish were added daily. In controls, only water was added.

those of the other species, which makes it more likely to be preyed upon by the crayfish. *L. varians* was the only species that tended to reduce its activity with crayfish chemical cues compared to controls (Fig. 1), and this reduction was significant if this species was analyzed separately (results not shown).

Some caution is needed in translating laboratory results (particularly involving single chemicals) to natural conditions (KOHLER 1992). Concentration of chemical cues in experiments is likely to be higher than those existing in the field, except perhaps under very low flow conditions, when densities of animals may be high and habitat availability low (HEARNDEN & PEARSON 1991). Under natural conditions, complex mixes of diverse chemical cues with patchy distributions arise due to varied physical environments, stimuli, biota and spatial and temporal flow dynamics (BRONNMARK & HANSSON 2000). However, shredders are found mostly in pools, which may represent a less complex habitat compared with riffles, where concentrations and movement of chemicals are diluted and diverted by water flow and substrate structure (BURKS & LODGE 2002).

This preliminary study suggests that it would be useful to explore further the possible medium- to long-term effects of chemical cues, using a longer experiment with a range of concentrations and different frequencies of introduction of cues.

ACKNOWLEDGEMENTS

We are grateful to Mikis Bastian and Regina Camacho, who helped in the field. L. Boyero was supported by a postdoctoral grant from the Secretaría de Estado de Educación y Universidades (MECD, Spain) co-financed by the European Social Fund.

REFERENCES

Boyero L. & Pearson R.G. 2006. Intraspecific interference in a tropical stream shredder guild. *Marine and Freshwater Research* 57: 201-206.

Boyero L., Pearson R.G. & Camacho R. 2006a. Leaf processing in Australian tropical streams: the role of different species on ecosystem functioning. *Archiv für Hydrobiologie* 166: 453-466.

Boyero L., Ramírez A., Dudgeon D. & Pearson R.G. 2009. Are tropical streams really different? *Journal of the North American Benthological Society* 28: 397-403.

Boyero L., Rincón P.A. & Bosch J. 2006b. Case selection by a limnephilid caddisfly *Potamophylax latipennis* Curtis in response to different predators. *Behavioral Ecology and Sociobiology* 59: 364-372.

Boyero L., Rincón P.A. & Pearson R.G. 2008. Effects of a predatory fish on a tropical detritus-based food web. *Ecological Research* 23: 649-655.

Bronnmark C. & Hansson L. 2000. Chemical communication in aquatic systems, an introduction. *Oikos* 88: 103-109.

Burks R. & Lodge D. 2002. Cued in, advances and opportunities in freshwater chemical ecology. *Journal of Chemical Ecology* 28: 1901-1915.

Cheshire K., Boyero L. & Pearson R.G. 2005. Food webs in tropical Australian streams: shredders are not scarce. *Freshwater Biology* 50: 748-769.

Chivers D.P., Wiseden B.D. & Smith J.F. 1996. Damselfly larvae learn to recognize predators from chemical cues in the predator's diet. *Animal Behaviour* 52: 315-320.

Cross W. & Benke A. 2002. Intra- and interspecific competition among coexisting lotic snails. *Oikos* 96: 251-264.

Dobson M., Mathooko J.M., Magana A. & Ndegwa F.K. 2002. Macroinvertebrate assemblages and detritus processing in Kenyan highland streams, more evidence for the paucity of shredders in the tropics? *Freshwater Biology* 47: 909-919.

Graça M. 2001. The role of invertebrates on litter decomposition in streams — a review. *International Review of Hydrobiology* 86: 383-393.

Harding J. 1997. strategies for coexistence in two species of New Zealand Hydropsychidae (Trichoptera). *Hydrobiologia* 350: 25-33.

Hearnden M. & Pearson R.G. 1991. Habitat partitioning among the mayfly species (Ephemeroptera) of Yuccabine Creek, a tropical Australian stream. *Oecologia* 87: 91-101.

Hemphill N. 1988. Competition between two stream dwelling filter-feeders, *Hydropsyche oslari* and *Simulium virgatum*. *Ecological Monographs* 77: 73-80.

Huryn A. & Chivers D. 1999. Contrasting behavioural responses by detritivorous and predatory mayflies to chemicals released by injured conspecifics and their predators. *Journal of Chemical Ecology* 25: 2729-2739.

Jonsson M. & Malmqvist B. 2003. Mechanisms behind positive diversity effects on ecosystem functioning: testing the facilitation and interference hypotheses. *Oecologia* 134: 554-559.

KOHLER S. 1992. Competition and the structure of a benthic stream community. *Ecological Monographs* 62: 165-188.

KUHARA N., NAKANO S. & MIYASAKA H. 2000. Alterations in the grazing activities of cased caddisfly larvae in response to variation in predation risk and resource level. *Ecological Research* 16: 705-714.

MCAULIFFE J. 1984. Competition for space, disturbance, and the structure of a benthic stream community. *Ecology* 65: 894-908.

MCCARTHY T. & FISHER W. 2000. Multiple predator-avoidance behaviours of the freshwater snail *Physella heterostropha pomila*: responses vary with risk. *Freshwater Biology* 44: 387-397.

MCINTOSH A., PECKARSKY B. & TAYLOR B. 1999. Rapid size-specific changes in the drift of *Baetis bicaudatus* (Ephemeroptera) caused by alterations in fish odour concentration. *Oecologia* 118: 256-264.

MCINTOSH A., PECKARSKY B. & TAYLOR B. 2004. Predator-induced resource heterogeneity in a stream food web. *Ecology* 85: 2279-2290.

MIYASAKA H., GENKAI-KATO M., KUHARA N. & NAKANO, S. 2003. Predatory fish impact on competition between stream insect grazers: a consideration of behaviourally- and density-mediated effects on an apparent coexistence pattern. *Oikos* 101: 511-520.

PEARSON R., BENSON L. & SMITH R. 1986. Diversity and abundance of the fauna in Yuccabine Creek, a tropical rainforest stream, pp. 329-342. In: DeDeckker P. & Williams W., Edits. Limnology in Australia. *Melbourne: CSIRO*.

PEARSON R. G. & TOBIN R. 1989. Litter consumption by invertebrates from an Australian tropical rainforest stream. *Archiv für Hydrobiologie* 116: 71-80.

PECKARSKY B., MCINTOSH A., TAYLOR B. & DAHL T. 2002. Predator chemical induce changes in mayfly life history traits: a whole-stream manipulation. *Ecology* 83: 612-618.

PECKARSKY B. & TAYLOR B. 2004. Predator-induced resource heterogeneity in a stream food web. *Ecology* 85: 2279-2290.

PECKARSKY B., TAYLOR B., MCINTOSH A., MCPEEK M. & LYTLE D. 2001. Variation in mayfly size at metamorphosis as a developmental response to risk of predation. *Ecology* 82: 740-757.

PIJANOWSKA J. & KOWALCZEWSKI A. 1997. Cues from injured *Daphnia* and from cyclopoids: feeding on *Daphnia* can modify life histories of conspecifics. *Hydrobiologia* 350: 99-103.

POLLOCK M. & CHIVERS D. 2004. The effects of density on the learned recognition of heterospecific alarm cues. *Ethology* 110: 341-349.

SCRIMGEOUR G., CULP J. & CASH K. 1994. Anti-predator responses of mayfly larvae to conspecific and predator stimuli. *Journal of the North American Benthological Society* 13: 299-309.

SHORT T. & HOLOMUZKI J. 1992. Indirect effects of fish on foraging behaviour and leaf processing by the isopod *Lirceus fontinalis*. *Freshwater Biology* 27: 91-97.

TURNER A., BERNOT R. & BOES C. 2000. Chemical cues modify species interactions: the ecological consequences of predator avoidance by freshwater snails. *Oikos* 88: 148-158.